# Response of C:N:P in the plant-soil system and stoichiometric homeostasis of *Nitraria tangutorum* leaves in the oasis-desert ecotone, Northwest China

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**Abstract:** *Nitraria tangutorum* nebkhas are widely distributed in the arid and semi-arid desert areas of China. The formation and development of *N. tangutorum* nebkhas are the result of the interaction between vegetation and the surrounding environment in the process of community succession. Different successional stages of *N. tangutorum* nebkhas result in differences in the community structure and composition, thereby strongly affecting the distribution of soil nutrients and ecosystem stability. However, the ecological stoichiometry of *N. tangutorum* nebkhas in different successional stages remains poorly understood. Understanding the stoichiometric homeostasis of *N. tangutorum* could provide insights into its adaptability to the arid and semi-arid desert environments. Therefore, we analyzed the stoichiometric characteristics of *N. tangutorum* in four successional stages, i.e., rudimental, developing, stabilizing, and degrading stages using a homeostasis model in an oasis-desert ecotone of Northwest China. The results showed that soil organic carbon (SOC), total nitrogen (TN), and total phosphorus (TP) contents and their ratios in the 0–100 cm soil depth were significantly lower than the averages at regional and global scales and were weakly influenced by successional stages in the oasis-desert ecotone. TN and TP contents and C:N:P in the soil showed similar trends. Total carbon (TC) and TN contents in leaves were 450.69–481.07 and 19.72–29.35 g/kg, respectively, indicating that leaves of *N. tangutorum* shrubs had a high storage capacity for C and N. Leaf TC and TN contents and N:P ratio increased from the rudimental stage to the stabilizing stage and then decreased in the degrading stage, while the reverse trend was found for leaf C:N. Leaf TP content decreased from the rudimental stage to the degrading stage and changed significantly in late successional stages. N:P ratio was above the theoretical limit of 14, indicating that the growth of *N. tangutorum* shrubs was limited by P during successional stages. Leaf N, P, and N:P homeostasis in four successional stages was identified as "strictly homeostasis". Redundancy analysis (RDA) revealed that soil acidity (pH) and the maximum water holding capacity were the main factors affecting C:N:P stoichiometric characteristics in *N. tangutorum* leaves. Our study demonstrated that *N. tangutorum* with a high degree of stoichiometric homeostasis could better cope with the arid desert environment.

**Keywords:** nebkhas; ecological stoichiometry; ecological adaptability; successional stages; arid area

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## 1 Introduction

Ecological stoichiometry, generally referring to carbon (C), nitrogen (N) and phosphorus (P) in terrestrial ecosystems, is defined as the balance of multiple chemical elements and their interactions in the ecosystem (Schindler, 2003; Li et al., 2017; Bai et al., 2019). Previous studies of ecological stoichiometry have focused on population dynamics, individual growth, community succession, nutrient limitation, and ecosystem stability (Elser et al., 2000a; Abbas et al., 2013). C is a structural element that acts as the substrate and energy source for various physiological and biochemical processes in plants (Liu et al., 2011). N and P are functional limiting factors that partly determine plant utilization strategy and survival adaptation (Güsewell, 2005; Elser et al., 2007). C:N:P stoichiometry of terrestrial ecosystems has been used to explore the relationships and feedbacks between soil and plant components of ecosystems (Ren et al., 2016). Previous research has mainly focused on the C:N:P stoichiometry in leaves or soil, with less attention paid to the plant-soil interactions (Wang et al., 2015; Piaszczyk et al., 2019).

Stoichiometric homeostasis refers to the ability of biological organisms to maintain relatively stable chemical metrology regardless of environmental changes, reflecting the adaptability of physiology and biochemistry to changes in the external environment (Koojiman, 1995; Frost and Elser, 2002). Stoichiometric homeostasis is not only related to plant species, plant organs, and nutrient supply, but also to plant growth stages (Yu et al., 2011). Plants that maintain a strong stoichiometric homeostasis are more conservative in the utilization of nutrients, while plants with a weaker stoichiometric homeostasis are more adaptable to changes in the environment (Persson et al., 2012). Therefore, stoichiometric homeostasis of plants can be used as a predictive tool for determining the adaptability of plants to the external environment.

Oasis-desert ecotones are not only transitional zones connecting oasis and desert ecosystems, but also important sites for material circulation, energy conversion, and information transmission between these two systems (Mao et al., 2014; Xiao et al., 2019). Due to the double influence of oasis and desert systems, the area where *N. tangutorum* shrubs grow has become quite sensitive to the environmental changes. A nebkha is a vegetation-influenced aeolian sedimentary landform (Tengberg, 1995). *N. tangutorum* nebkhas are the result of the interaction between vegetation and the desert environment during community succession in arid and semi-arid regions (Khalaf et al., 1995). *N. tangutorum* nebkhas can effectively intercept and immobilize large amounts of wind-eroded materials and prevent quicksand from invading the oasis, meaning that the plant plays an important role in protecting biodiversity, inhibiting desertification, and maintaining ecological security and internal stability of the oasis (Su et al., 2007; Eziz et al., 2010). Therefore, studying the succession of *N. tangutorum* nebkhas is essential for assessing ecosystem damage and developing restoration strategies.

The succession of nebkhas is a dynamic equilibrium process in which plants, wind, and sand interact (Hesp, 1983). Normally, there are four successional stages: rudimental, development, stabilizing and degrading stages (Tengberg, 1995; Tengberg and Chen, 1998; Du et al., 2010). During the succession process, the morphology of nebkhas changes continuously as the vegetated shrubs grow and develop. In the windblown sand, the shrubs intercept sand particles containing clay and silt, and then shrub litter is deposited and decomposed on the surface of the sand mound (Li et al., 2013; Luo et al., 2016). After a long-term accumulation, the sand mound eventually leads to the enrichment of soil nutrients under the shrubs and the formation of fertile islands (Zhou et al., 2015). The intensity of the fertilizer island effect is affected by factors such as shrub plant density, crown size, topography, and successional stages, resulting in gradient changes in soil nutrients in the nebkhas (Li et al., 2017). The nebkhas are formed by complex processes of plant-soil-atmosphere interactions in arid and semi-arid regions. Although previous studies have extensively investigated nebkhas, a comprehensive study of the plant-soil composite system of nebkhas, the variation in soil nutrients in nebkhas in different successional stages and soil depths, and the relationship between C, N, P, and other soil nutrients are neglected. The lack of understanding of vegetation shrubs' ecological adaptability in arid and semi-arid regions has restricted the accurate formulation and implementation of ecological restoration strategies in the

region.

Based on previous studies, we analyzed the characteristics of C, N, and P in the leaf-soil system as well as the stoichiometric homeostasis of *N. tangutorum* nebkhas in the oasis-desert ecotone in Inner Mongolia Autonomous Region, China. Our objectives were (1) to determine the variation in C, N, and P contents of *N. tangutorum* in the leaf-soil system in different successional stages; (2) to explore the relationship between C, N, and P contents in the leaf-soil system in *N. tangutorum* nebkhas; and (3) to study the characteristics of stoichiometric homeostasis in different successional stages of *N. tangutorum* nebkhas.

## 2 Materials and methods

### 2.1 Study area

The study area was located in the oasis-desert ecotone in Jilantai Town, Inner Mongolia Autonomous Region, China (39°40′49″–39°41′22″N, 105°45′30″–105°45′39″E). The region typically has fixed dunes without human disturbance. The average elevation is 1020–1030 m a.s.l. The study area has a temperate continental monsoon climate characterized by scarce precipitation, strong evaporation, hot summer, and cold winter. The annual average temperature is 8.60°C. The extreme maximum temperature is 40.90°C, the extreme minimum temperature is –31.20°C, and mean annual precipitation is 102.20 mm, with 61.38% of the rainfall occurring between July and September (1965–2019; Fig. 1). The average annual evaporation is about 3006 mm, and the annual sunshine is 3316 h. The prevailing winds are northwest and west-northwest, the latter being the principal damaging wind, with an average annual speed of 3.54 m/s. The maximum wind speed is 15.00 m/s, and the mean annual number of days with strong winds is 34 d. The soil type is an aeolian sandy soil. Mean soil moisture content is 0.48%–0.86%, the soil density is 1.58–1.63 g/cm$^3$, the soil pH is 8.90–9.22, and the soil maximum water holding capacity is 21.95%–30.54% in all cases. With *N. tangutorum* as the dominant species, the mean density of *N. tangutorum* nakbhas is 48 individuals/hm$^2$. The associated plant species mainly grow in the inter-dune area and include *Artemisa arenaria*, *Elymus dahuricus* and *Agriophyllum squarrosum*.

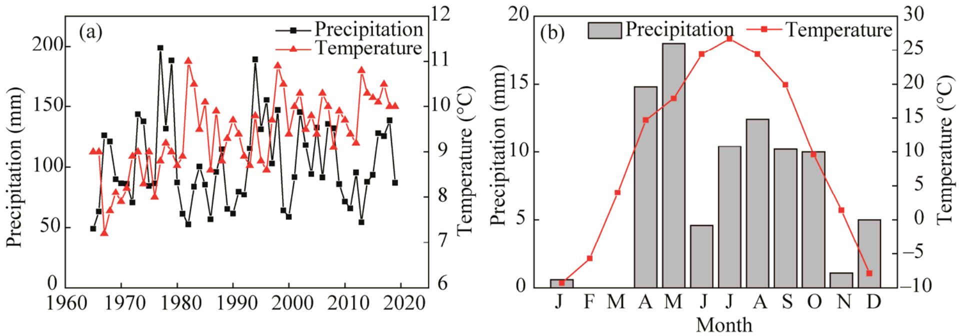


**Fig. 1** Mean precipitation and temperature in different years (a) and months (b) of the study area

### 2.2 Experimental design and methods

In late August 2019, according to the descriptions of Du et al. (2009) and the actual situation of sample plots, we investigated the rudimental, developing, stabilizing, and degrading stages of *N. tangutorum* nebkhas. We set three standardized quadrats (100 m×100 m) with discernable gradients of vegetative succession in a fixed dune. Three *N. tangutorum* nebkhas were selected in each successional stage and each sample plot, for a total of 36 sample nebkhas. The main nebkha and vegetation characteristics measured were the long axis, short axis, height, death rate of branches, and vegetation coverage. Five small quadrats (1 m×1 m) were set in each successional stage for a total of 20 quadrats, and these were chosen to determine coverage and vegetation diversity. Each small quadrat was used to record coverage and species number of *N. tangutorum* nebkhas (Table 1).

**Table 1** Characteristics of *Nitraria tangutorum* nebkhas in different successional stages

| Successional stage | Long axis (m) | Short axis (m) | Height (m) | Plant height (cm) | Death rate of branches (%) | Coverage (%) | Species number | Plant species | Plant shape |
|---|---|---|---|---|---|---|---|---|---|
| Rudimental stage | 3.95±0.47[b] | 3.22±0.44[b] | 0.59±0.03[c] | 33.33±1.11[d] | 0.00[c] | 34.00±2.67[c] | 2 | *N. tangutorum*, *Agriophyllum squarrosum* | Irregular shape |
| Developing stage | 5.03±0.50[ab] | 4.02±0.25[ab] | 0.81±0.06[b] | 72.00±2.00[a] | 9.00±1.33[bc] | 45.67±2.89[b] | 3 | *N. tangutorum*, *Artemisa arenaria*, *A. squarrosum* | Semi-ellipse |
| Stabilizing stage | 6.17±0.42[a] | 4.48±0.21[a] | 1.32±0.05[a] | 61.33±2.89[b] | 21.33±2.4[b] | 60.33±3.11[a] | 4 | *N. tangutorum*, *A. arenaria*, *Elymus dahuricus*, *A. squarrosum* | Semi-ellipse |
| Degrading stage | 5.08±0.61[ab] | 4.51±0.20[a] | 0.92±0.09[b] | 43.00±2.67[c] | 53.33±7.78[a] | 35.67±4.22[bc] | 3 | *N. tangutorum*, *A. arenaria*, *A. squarrosum* | Semi-oval |

Note: Different lowercase letters within the same row represents significant differences among different successional stages ($P<0.05$ level). Means±SD; $n=9$.

In each sample plot, soil samples from 100 cm-deep profiles were collected in different successional stages, with soil samples taken at 0–5, 5–10, 10–20, 20–30, 30–50, 50–70, and 70–100 cm soil depths. Then, soil samples with the same successional stage and soil depth in a plot were mixed evenly. Each plot had three replicates. Soil samples were put in sealed plastic bags and air-dried in the shade for approximately 7 d. After sieving through a 2-mm mesh sieve, we analyzed soil samples for acidity (pH) and particle size distribution (0–5 cm). The samples were sieved through a 0.15-mm mesh sieve, ground with a ball mill, and analyzed for soil organic carbon (SOC), total nitrogen (TN), and total phosphorus (TP). Simultaneously, soil bulk density, water moisture, capillary porosity, and non-capillary porosity were measured at 6 soil depths in 36 *N. tangutorum* nebkhas by using a cutting ring (100 $cm^3$).

Sun-exposed fully expanded and healthy mature leaves were collected from four directions (windward slope, leeward slope, and two sides). Six individuals of different successional stages (>100 g fresh mass) at each plot were mixed uniformly and individually placed in paper envelopes for subsequent analyses. A total of 36 leaf samples (4 successional stages×3 quadrats×3 replicates) were collected and oven-dried for 30 min at 105°C and then dried at 65°C for approximately 48 h to a consistent weight. The dried leaves were ground into a fine powder using a ball mill (MM200, Retsch, Haan, Germany) and sieved through a 0.15-mm mesh sieve; then those samples were used for the determination of total carbon (TC), TN, and TP contents in the leaves.

### 2.3 Methods

Soil moisture and bulk density were determined by using stainless steel cylinders (100 $cm^3$). Soil pH was measured by using a soil:water ratio of 1.0:2.5 with a pH meter (STARTER 3100, USA). Particle size distribution was determined by a laser diffraction particle size analyzer (Mastersizer 3000, UK). Soil maximum water holding capacity, comprising soil capillary water holding capacity and soil non-capillary water holding capacity, is defined as the soil water content when all soil pores are filled with water. Soil maximum water holding capacity was determined through immersion in water for 12 h and then weighing immediately. Soil SOC and TC in plants were tested by the $K_2Cr_2O_7$-$H_2SO_4$ oxidation method (Ren et al., 2015). TN in soil and leaves was determined by the Kjeldahl acid-digestion method and micro-Kjeldahl method, respectively (Bao, 2010). TP in soil and leaves was tested by using $H_2SO_4$-$HClO_4$ (Romanyà et al., 2017) and $H_2SO_4$-$H_2O_2$ digestion methods, respectively, using an ultraviolet spectrophotometer (UV-2450, Shimadzu, Japan) (Mendes et al., 2017).

### 2.4 Statistical analysis

The strength of plant stoichiometric homeostasis was measured by the homeostatic coefficient $1/H$ (Sterner and Elser, 2002). Regression analyses were conducted for C, N, P, and their ratios in

leaves in successional stages. Owing to the slope expected to be equal to or greater than 0.00, we used one-tailed tests with $\alpha$=0.10. If the regression relationship was not significant ($P$>0.10), $1/H$ was set to zero, and the organism was considered to be "strictly homeostatic". Species with $1/H$ =1.00 were considered as not homeostatic (Li et al., 2014; Bai et al., 2019). If the regression relationship was significant, $1/H$ in the interval from 0.00 to 1.00 could be divided into $0.00<1/H<0.25$, "homeostatic"; $0.25<1/H<0.50$, "weakly homeostatic"; $0.50<1/H<0.75$, "weakly plastic"; and $1.00/H>0.75$, "plastic" (Persson et al., 2012). The formula of the model is as follows:

$$Y = cX^{\frac{1}{H}}, \tag{1}$$

$$\ln Y = \frac{1}{H}\ln X + \ln c, \tag{2}$$

where $Y$ are the C, N, and P contents (g/kg) or the C:N, C:P, and C:P ratios in the leaves of *N. tangutorum*; $X$ are the C, N, and P contents (g/kg), or the C:N, C:P, and C:P ratios in the soil; and c is a constant.

Excel 2016 was used to sort the experimental data. SPSS 19.0 (SPSS, Inc., Chicago, IL, USA) was used to analyze the data. One-sample Kolmogorov-Smirnov tests (K-S) were used to analyze the contents of C, N, P, and ecological stoichiometry in the soil and leaves in different successional stages. One-way analysis of variance (ANOVA) was conducted to explore significant differences in these factors in different successional stages. Significant differences were determined at the 0.05 level. Redundancy analysis (RDA) was conducted using Canoco 5.0 (Biometry, Wageningen, Netherlands). Figures were drawn with Origin 9.0 (Origin Lab, Northampton, MA, USA).

## 3 Results

### 3.1 Soil nutrient contents and C:N:P ratios in different successional stages

Average SOC, TN, and TP contents in the soil followed the order of stabilizing stage>developing stage>degrading stage>rudimental stage. The successional stage had no effect on SOC, TN, or TP content in the soil (Fig. 2a–c). SOC content at 0–5 cm depth increased by 39.63% the succession. SOC content at 10–20 and 20–30 cm soil depths increased by 96.37% and 68.08% from the rudimental stage to the stabilizing stage, respectively ($P$<0.05). However, SOC content was not significantly different among 5–10, 30–50, 50–70, and 70–100 cm soil depths throughout the succession ($P$>0.05; Fig. 2a). TN contents at 20–30 and 50–70 cm depths increased by 64.74% and 36.85% from the rudimental stage to the degrading stage ($P$<0.05). The difference was not significant among 0–5, 5–10, 10–20, 30–50, and 70–100 cm soil depths throughout the succession ($P$>0.05; Fig. 2b). Compared with the rudimental stage, TP content increased by 32.88%, 42.50%, and 25.41% at 20–30 cm depth and reached a peak in the stabilizing stage. TP content at 0–5, 5–10, 10–20, 30–50, 50–70, and 70–100 cm depths was not significantly different among successional stages ($P$>0.05; Fig. 2c). In general, SOC, TN, and TP contents were stable below 30 cm depth.

The successional stage had no effect on C:N, C:P, or N:P ratios in the soil. C:N ratio at 0–5 and 20–30 cm depths fluctuated markedly along the gradient of vegetative succession, increased by 48.72% at 0–5 cm depth, and decreased by 91.82% at 20–30 cm depth throughout the succession ($P$<0.05). At 5–10, 10–20, 30–50, 50–70, and 70–100 cm depths, C:N ratio was not significantly different among successional stages ($P$>0.05; Fig. 2d). Compared with the rudimental stage, C:P ratios in the developing stage at 0–5 cm depth were increased by 53.72% ($P$<0.05). The ratios were not significantly different at 5–10, 10–20, 30–50, 50–70, or 70–100 cm soil depths throughout the succession ($P$>0.05; Fig. 2e). Compared with the rudimental stage, N:P ratios in the degrading stage at 20–30 cm depth increased by 41.46% ($P$>0.05). At 5–10, 10–20, 30–50, 50–70, and 70–100 cm depths, N:P ratio was not significantly different among successional stages ($P$>0.05; Fig. 2f). Consequently, C:N, C:P, and N:P ratios remained stable below 30 cm.

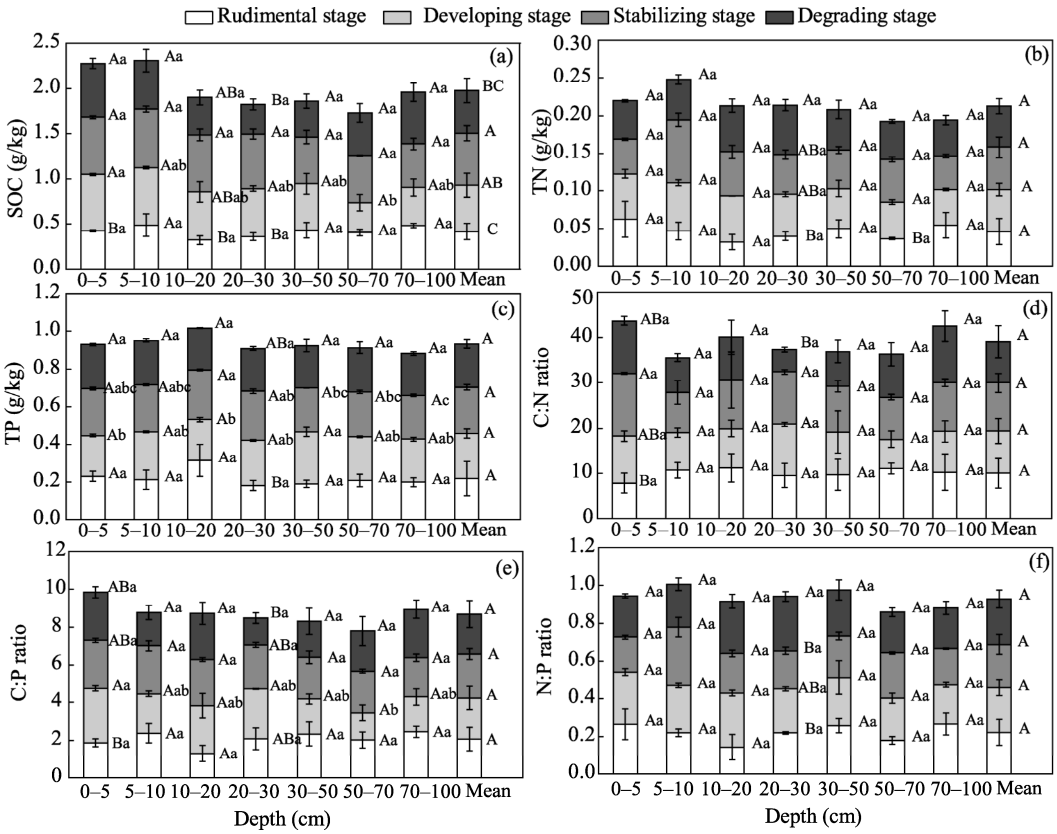


**Fig. 2** Stoichiometric characteristics of C (a), N (b), and P (c) and their ratios (d–f) at different soil depths and successional stages. SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; bars indicate standard deviations. Different uppercase letters represent significant differences among different successional stages within the same soil depth ($P$<0.05 level); and different lowercase letters represent significant differences among different soil depths within the same successional stage ($P$<0.05 level).

### 3.2 Leaf nutrient contents and C:N:P ratios in different successional stages

Overall, successional stage had significant effects on the contents of TC, TN, TP, and C:N:P ratios in the leaves of *N. tangutorum*. The mean leaf TC, TN, and TP contents and C:N, C:P, and N:P ratios were 450.69–481.07 g/kg, 19.68–29.35 g/kg, 1.00–1.28 g/kg, 16.91–23.59, 367.63–450.74, and 15.71–24.22, respectively (Table 2). As vegetative succession progressed, TC and TN contents increased from the rudimental stage to the stabilizing stage and reached a peak in the stabilizing stage; the values increased by 4.20% and 48.83%, respectively ($P$<0.05). Surprisingly, the contents of TC and TN decreased in the degrading stage, and they were not significantly different between the developing and stabilizing stages ($P$>0.05). TP content decreased with succession of *N. tangutorum*; leaf TP content dropped sharply by 27.00% in the degrading stage ($P$<0.05), and leaf TP content was not significantly different between the rudimental stage and the developing stage ($P$>0.05). Leaf C:N ratio in the rudimental stage was 1.27, 1.39, and 1.19 times higher than in the developing, stabilizing, and degrading stages, respectively ($P$<0.05). Leaf C:N ratio was not significantly different among the subsequent three stages ($P$>0.05). Leaf C:P and N:P ratios were increased by 23.85% and 49.19% from the rudimental stage to the degrading stage, respectively ($P$<0.05).

### 3.3 Stoichiometric homeostasis in the leaves of *N. tangutorum* in different successional stages

In general, the results from leaves showed that $1/H$ differed according to which elemental index was measured. For N and P homeostasis and N:P stoichiometric homeostasis, the leaves of *N.*

*tangutorum* in four successional stages were identified as "strictly homeostasis" ($P$>0.10; Fig. 3a–c).

**Table 2** Stoichiometric characteristics of leaf total carbon (TC), total nitrogen (TN), and total phosphorus (TP) and their ratios in different successional stages

| Successional stage | TC (g/kg) | TN (g/kg) | TP (g/kg) | C:N | C:P | N:P |
|---|---|---|---|---|---|---|
| Rudimental stage | 461.18±4.70$^{B}$ | 19.72±1.54$^{B}$ | 1.36±0.10$^{A}$ | 23.46±1.75$^{A}$ | 363.95±47.08$^{B}$ | 15.45±2.84$^{B}$ |
| Developing stage | 480.57±15.78$^{A}$ | 27.33±2.29$^{A}$ | 1.33±0.05$^{A}$ | 18.49±3.03$^{B}$ | 368.58±27.69$^{B}$ | 21.08±0.69$^{A}$ |
| Stabilizing stage | 481.07±5.68$^{A}$ | 29.35±4.76$^{A}$ | 1.24±0.04$^{B}$ | 16.91±3.23$^{B}$ | 397.65±29.52$^{B}$ | 24.22±4.12$^{A}$ |
| Degrading stage | 450.69±1.75$^{B}$ | 23.01±1.48$^{B}$ | 1.03±0.04$^{C}$ | 19.67±1.27$^{B}$ | 450.74±31.00$^{A}$ | 23.05±2.63$^{A}$ |

Note: Different uppercase letters within the same row represent significant differences of *N. tangutorum* leaves in different successional stages at $P$<0.05 level. Means±SD; $n$=9.

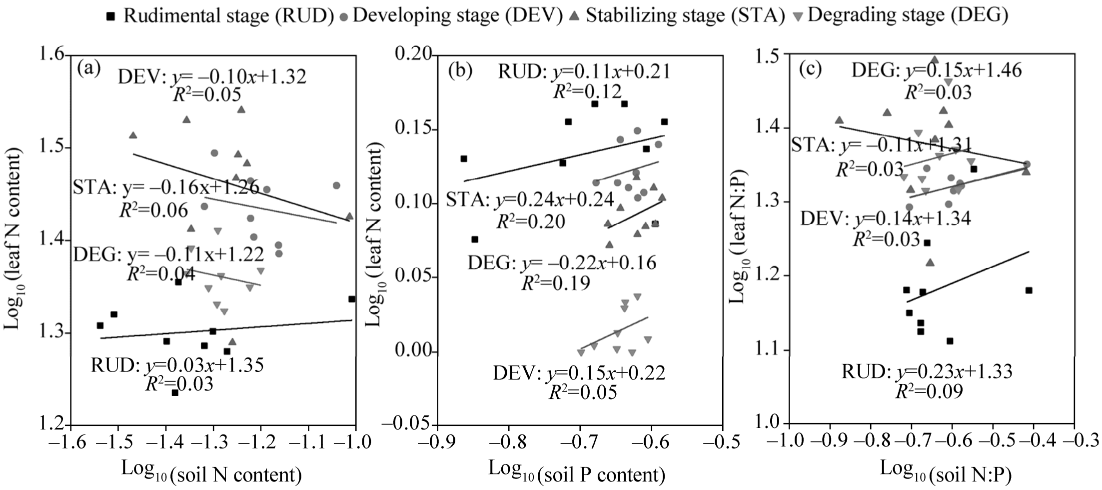


**Fig. 3** Relationships between log10-transformed nutrient contents and stoichiometry of N and P in the leaves of *N. tangutorum* in different successional stages

### 3.4 Relationships of nutrient contents in leaves and soil with C:N:P ratios

RDA analysis was preceded by a deterended correspondence analysis. When the maximum gradient of the sorting axis was 1.90, which was less than 3.00, an RDA analysis was performed to determine the relationship between physical-chemical factors and C:N:P ratios of *N. tangutorum* leaves. The results showed that the first two axes explained a total of 45.40% of the variation in leaf C:N:P stoichiometric characteristics. Leaf TC, TN, C:P, and N:P were significantly positively correlated with pH and soil maximum water holding capacity. Moreover, pH had significantly negative effects on leaf TP and C:N. Soil bulk density was positively correlated with leaf C:N and C:P and was negatively correlated with leaf TC, TN, TP, and N:P (Fig. 4).

The order of importance of soil physical-chemical factors for leaf nutrient contents and their ratios was as follows: pH>soil maximum water holding capacity>soil SOC>soil N:P>soil C:N>soil bulk density>soil moisture>soil TN>soil TP>soil C:P>capillary porosity. Soil pH and the maximum water holding capacity were the main factors affecting C:N:P stoichiometric characteristics in leaves, accounting for 42.8% and 17.5% of the variation, respectively (Table 3).

## 4 Discussion

Our results showed that from the rudimental stage to the degrading stage of *N. tangutorum* nebkhas, the mean soil SOC, TN, and TP contents were 0.42–0.58, 0.05–0.06, and 0.22–0.25 g/kg, respectively, which were lower than the global average levels (25.71, 2.10, and 0.36 g/kg) and the

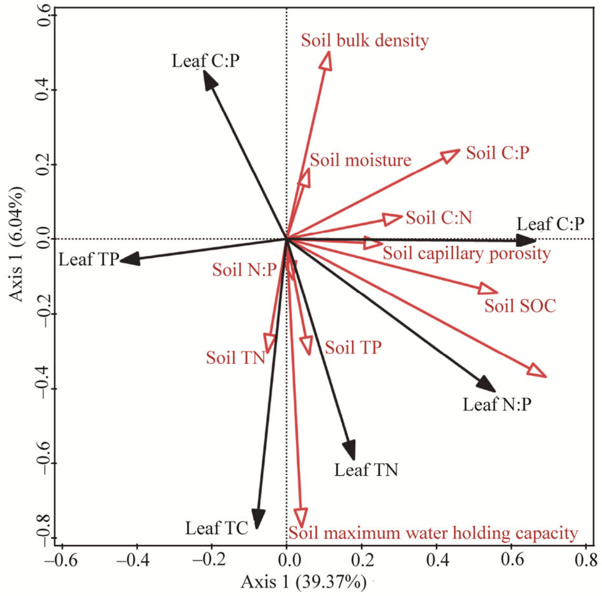


**Fig. 4** Redundancy analysis result of relationships between leaf C:N:P stoichiometric characteristics and soil physical-chemical factors. SOC, soil organic carbon; TN, total nitrogen; TC, total carbon; TP, total phosphorus.

**Table 3** Importance sequencing and Duncan's test of soil physical-chemical factors

| Soil physical-chemical factor | Interpretation (%) | Contribution (%) | Importance sequencing | *F* | *P* |
|---|---|---|---|---|---|
| pH | 19.7 | 42.8 | 1 | 8.3 | 0.004 |
| Soil maximum water holding capacity | 8.1 | 17.5 | 2 | 3.7 | 0.046 |
| Soil SOC | 1.5 | 3.4 | 3 | 0.7 | 0.444 |
| Soil N:P | 1.2 | 2.5 | 4 | 0.5 | 0.456 |
| Soil C:N | 2.2 | 4.7 | 5 | 1.0 | 0.314 |
| Soil bulk density | 1.7 | 3.6 | 6 | 0.7 | 0.376 |
| Soil moisture | 3.5 | 7.7 | 7 | 1.6 | 0.214 |
| Soil TN | 1.4 | 2.9 | 8 | 0.6 | 0.504 |
| Soil TP | 4.3 | 9.3 | 9 | 2.0 | 0.162 |
| Soil C:P | 2.4 | 5.3 | 10 | 1.1 | 0.298 |
| Capillary porosity | 0.1 | 0.2 | 11 | 0.1 | 0.934 |

Note: SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus.

national averages (29.51, 2.30, and 0.65 g/kg) (Tian et al., 2010; Xu et al., 2013). The reason for this pattern is mainly related to dry climatic conditions and frequent wind and sand activities in the region (Zhang et al., 2011). On the one hand, dry climatic condition with little rain and strong evaporation prevents soil water conservation, which limits the decomposition of soil organic matter to a certain extent and thus reduces the source of soil nutrients. On the other hand, soil fine particles are the carriers of soil nutrients. However, frequent windblown sand leads to the erosion of soil fine particles and surface litter in the *N. tangutorum* nebkhas in the transitional zone of the Jilantai Town, which is not conducive to the accumulation of nutrients, thus resulting in the overall low content of nutrients, such as SOC, soil TN, and TP in the *N. tangutorum* nebkhas. The spatial heterogeneity of soil nutrients in nebkhas is often associated with successional stage, soil depth, vegetation type, and landscape type (Du et al., 2009; Zhang et al., 2009; Rong et al., 2015; Cao et al., 2016; Gong et al., 2017; Wang et al., 2019). Our results showed that the order of soil SOC, TN, and TP contents in different successional stages was stabilizing stage>developing

stage>degrading stage>rudimental stage, and SOC and TN contents were much higher in the 0–10 cm depth than in the deeper layers ($P$>0.05). The variation in nutrient content of *N. tangutorum* nebkhas in different successional stages was mainly related to the growth status and vegetation cover of *N. tangutorum* shrubs (Li et al., 2010), where the vegetation cover of *N. tangutorum* nebkhas in the stabilizing stage was as high as 60.33% (Table 1), and the good growth status of *N. tangutorum* shrubs provided not only a nutrient source for *N. tangutorum* nebkhas but also a higher vegetation cover, leading to greater wind-proofing and sand-fixing capacity. More fine-grained materials are intercepted by *N. tangutorum* shrubs and are accumulated on the tops of the nebkhas (Table 4), thereby increasing the nutrient input to the topsoil (Yang et al., 2014; Li et al., 2015).

**Table 4** Partical fraction in the topsoil of *Nitraria tangutorum* nebkhas in different successional stages

| Particle fraction | Successional stage | | | |
|---|---|---|---|---|
| | Rudimental stage | Developing stage | Stabilizing stage | Degrading stage |
| Clay content (%) | 0.82±0.24$^{c}$ | 1.23±0.32$^{c}$ | 3.89±0.47$^{a}$ | 2.54±0.11$^{b}$ |
| Silt content (%) | 3.12±0.77$^{b}$ | 5.22±1.23$^{a}$ | 5.12±1.82$^{a}$ | 4.12±1.33$^{b}$ |
| Sand content (%) | 96.13±0.11$^{a}$ | 93.45±0.59$^{a}$ | 91.84±1.25$^{a}$ | 93.72±1.52$^{a}$ |

Note: Different lowercase letters within the same row represent significant differences of *N. tangutorum* in different successional stages at $P$<0.05 level. Means±SD; $n$=9.

Leaves are the most sensitive plant organs to environmental changes, and their nutrient content represents the nutritional status of plants (Reich and Oleksy, 2004). Our results indicated that TC and TN contents in *N. tangutorum* leaves were higher than the averages for global terrestrial plants (464.00 and 20.60 g/kg) (Elser et al., 2000b), indicating that C and N storage capacities in the leaves of *N. tangutorum* are higher (Niklas and Cobb, 2005). RDA analysis showed that leaf TC and TN contents were weakly correlated with SOC and TN contents. This was inconsistent with the results of Han et al. (2005), who found that the nutrient characteristics of soil had an important impact on the N and P contents of plants. However, other studies have found that TC and TN contents in plants do not come from the soil; instead, they are normally obtained from the atmosphere through photosynthesis (He et al., 2006; Munns and Tester, 2008). Leaf TC, TN, and TP contents were strongly influenced by successional stages. TC and TN contents first increased in the stabilizing stage and then decreased in the degrading stage, and this pattern was related to vegetation growth status and vegetation cover of *N. tangutorum* nebkhas in different successional stages. As *N. tangutorum* nebkhas succession progressed, *N. tangutorum* shrubs grew vigorously and the vegetation cover increased gradually, reaching a peak in the stabilizing stage. The good growth conditions for *N. tangutorum* shrubs are conducive to the leaves storing a large amount of nutrients such as C and N. However, for large nebkhas in the degrading stages, the shrubs are unable to absorb nutrients from the soil and gradually degrade or even die, leading to the gradual decrease of leaf TC and TN in *N. tangutorum* shrubs. Additionally, our data confirmed that TP content was 1.00 g/kg in leaves of *N. tangutorum* in the degrading stage and 1.17–1.22 g/kg in other successional stages, values that were similar to the national levels (1.21 g/kg) (Han et al., 2005), but lower than the global level (1.58 g/kg) (Elser et al., 2000b). Therefore, the growth of *N. tangutorum* may be limited by P elements in the degrading stage.

Soil C:N:P ecological stoichiometry did not show a gradient of spatial heterogeneity, suggesting that successional stage and soil depth had little effects on soil C, N, or P stoichiometry. This was inconsistent with previous research results (Du et al., 2009; Wang et al., 2019). The reason may be due to a long-term stable supply-demand balance existing between soil and vegetation in the successional process of *N. tangutorum* nebkhas, ultimately leading to stable ratios of soil C:N, C:P, and N:P (Gong et al., 2017). This result further implied that *N. tangutorum* shrubs had a relatively high internal stability mechanism that gives them the ability to deal with extreme environments such as drought and saline alkaline soils. In addition, the mean soil C:N, C:P, and N:P ratios were 9.07–10.63, 2.06–2.35, and 0.22–0.24 in the 0–100 cm soil depth, respectively, which were lower than national average levels (11.90, 61.00, and 5.20) (Tian et al., 2010). The lower ratio of soil nutrient was attributed to reduced feedback of plant litter to the soil

in the study area, thus leading to poor soil nutrient levels with low organic matter content in the soil (Wang et al., 2019).

Leaf C:N, C:P, and N:P ratios of *N. tangutorum* nebkhas varied significantly among successional stages, which could be attributed to the difference in nutrient utilization strategies in the ontogeny of *N. tangutorum* shrubs (Li et al., 2013). In addition, leaf C:N ratio ranged from 17.91 to 23.69, with an average of 20.40, being lower than the global C:N ratio (23.40) (Kattge et al., 2011) and C:N ratio (21.20) of plant leaves in an arid areas (Li et al., 2013). Leaf C:P ratio ranged from 388.98 to 455.10 with an average of 416.00, being higher than the global level (232.00) (Kattge et al., 2011). This study demonstrated that *N. tangutorum* shrubs have high N utilization efficiency and lower P utilization efficiency in the oasis-desert ecotone (Gong et al., 2017). In extremely arid and nutrient-poor environments, *N. tangutorum* shrubs resist environmental stress by increasing the leaf C content (Rong et al., 2015). However, our study showed that N:P ratio of *N. tangutorum* was between 17.91 and 23.69, with an average of 21.24, indicating that *N. tangutorum* growth was limited by P during successional process (Koerselman and Meuleman, 1996; Li et al., 2016). The combined effect of soil and the atmospheric environment might result in the limited P nutrient. First, we speculated that *N. tangutorum* shrubs increased leaf C and N contents to survive under extreme drought and high temperature stress environments. The relatively low leaf P content resulted in a higher N:P ratio. Second, the lower P content in the soil resulted in less P absorbed by the roots of *N. tangutorum* (Wang et al., 2014), resulting in a higher N:P ratio.

RDA analysis showed that soil pH and soil maximum water holding capacity were the main factors affecting C:N:P stoichiometry of *N. tangutorum* leaves. Moreover, soil pH was positively correlated with TC and TN and negatively correlated with TP in leaves, indicating that suitable salinity promoted the accumulation of TC and TN in *N. tangutorum* leaves, decreased the absorption of TP, and led to increases in the ratios of C:N and C:P (Gong et al., 2017). In addition, anions such as $Cl^-$ and $SO_4^{2-}$ are present in large quantities in the soil. These anions compete with P, and the competition reduces the absorption of P by *N. tangutorum* (Rong et al., 2015). Therefore, the level of TP in the leaves of *N. tangutorum* was lowered, resulting in a higher N:P ratio. The soil moisture status in the study area also affects the nutrient status of the vegetation (Wang et al., 2019). This study showed that soil maximum water holding capacity was significantly positively correlated with leaf TC, TN, and TP, indicating that soil maximum water holding capacity is conducive to nutrient accumulation in *N. tangutorum* leaves. The azonal soil in the study is an aeolian sandy soil, and soil maximum water holding capacity was calculated as 21.95%–30.54%, with a poor water retention capacity in different successional stages. The decrease of soil maximum water holding capacity will result in the failure of timely infiltration of precipitation and an accompanying decrease in soil water content. Water scarcity limits utilization of soil nutrients by *N. tangutorum* shrubs and is detrimental to the accumulation of TC, TN, and TP in *N. tangutorum* leaves. However, the leaves of plants such as *N. tangutorum* have a large number of chloroplasts and a unique drought-resistant morphological structure, and the abundant light in desert areas provides strong photosynthetic properties for the leaves, thereby facilitating the large storage of TC; at the same time, drought can strengthen the plant's protective system and promote the increases of TN and TP in the leaves. A high N content can increase the concentration of plant cytosol, increase leaf water potential, promote water uptake, and alleviate drought stress (Aerts, 1996).

In the present study, we demonstrated that the degree of stoichiometric homeostasis is independent of both element variety and successional stages of *N. tangutorum* shrubs, to some extent reflecting their common strategies in nutrient allocation and environmental adaptation (Gu et al., 2017). Leaf N, P, and N:P were classified as "strictly homeostasis", a result that differed from the finding of Wang et al. (2019), who found that P and N:P stoichiometry in leaves was related to plant growth and development. Although the growth of *N. tangutorum* is restricted by P, *N. tangutorum* shrubs can regulate the effectiveness and utilization efficiency of limiting elements through a variety of physiological and biochemical mechanisms and are therefore able to maintain slow growth in response to the arid and P-limited environment (Persson et al., 2012). The stoichiometric homeostasis of N, P, and N:P in some plant leaves was negative, and the strength of stoichiometric homeostasis is generally characterized by the absolute value of the equilibrium

coefficient 1/*H* (Xing et al., 2015). The ranges of leaf $1/H_N$ (0.03–0.16), leaf $1/H_P$ (0.11–0.24) and leaf $1/H_{N:P}$ (0.14–0.23) for the four successional stages and the leaf N:P ratio were less variable than leaf N and P contents, indicating that leaf N:P was more stable than leaf N and P contents individually (Jiang et al., 2014). According to the growth rate hypothesis, fast-growing organisms have high P content and low biomass C:P and N:P ratios because biota need more P to be distributed to ribosomal RNA to maintain a higher growth rate and greater flexibility for leaf stoichiometric traits (Elser et al., 2003; Persson et al., 2012). In conclusion, in this study, *N. tangutorum* shrubs showed lower variations in leaf $1/H_N$, $1/H_P$, and $1/H_{N:P}$ than herbs ($1/H_N$: 0.13–0.28, $1/H_P$: 0.18–0.38 and $1/H_{N:P}$: 0.09–0.38) (Yu et al., 2010; Yu et al., 2011); this may be driven by the variation in plant life history. Slow-growing woody plants may be the dominant species with relatively conservative stoichiometric characteristics (Wang et al., 2018).

## 5 Conclusions

The current study showed that the soil SOC, TN, and TP contents in *N. tangutorum* nebkhas were lower than the national and global average levels. The successional stage and soil depth of *N. tangutorum* nebkhas had little effect on soil C, N, or P sequestration. However, TC, TN, and TP contents and stoichiometry in leaves were higher than the national and global average levels, and *N. tangutorum* growth was restricted by P shortage. The leaf N, P, and N:P stoichiometry in four successional stages were identified as "strictly homeostasis", indicating that *N. tangutorum* shrubs were more adapted to the oasis-desert ecotone in Jilantai Town, China. The pH and soil maximum water holding capacity were found to be the main factors affecting the C:N:P stoichiometry characteristics in the leaves of *N. tangutorum*. Despite this, our results highlighted the importance of an overall understanding of the nutrient cycling of leaf-soil systems and the adaptation strategies of *N. tangutorum* shrubs during the development of the nebkhas. This information may improve our understanding of the leaf-soil system of *N. tangutorum* in different successional stages in the oasis-desert ecotone.

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